SOME LIGHT REACTIONS OF THE MEDUSA GONIONEMUS.

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In the following notes it is my purpose to record some observations I have made on the behavior of *Gonionemus*[1] to light, after the experiments made a few summers ago on the reactions of its subumbral papillæ to light, and to include in the discussion points on which other observers are not agreed. I shall refer only to these publications.

After observing the behavior of *Gonionemus* for a considerable time the following brief statements will be found to hold concerning their habits. As darkness approaches the medusæ become restless in their native haunts where they are either lying inverted on the bottom, the apex of the bell being heavier, or clinging to plants and other submerged objects. Although all the tentacles in this species have adhesive pads near the free end, yet the animals attach by only a few, the remaining tentacles being spread out in all directions ready to catch their passing prey. When still daylight above the water it is becoming dusk, we may say, at their depth, and among the plants from one half to several meters deep. Within an hour after dark the eggs and sperm are deposited and their intermingling in the sea water increases many times their chance of development. Thus their locomotion in early evening is of great value as then more eggs will be fertilized. The dehiscence of the eggs and sperm has been shown to be due to the diminution or withdrawal of light, and seems rather direct evidence of an external stimulus causing a physiological change. For considerable time after the dehis-

[1] There would seem to be no need of stating that the Woods Hole species is the one under consideration. The experiments on which these notes are based were made at the Marine Biological Laboratory, at intervals between other work in the summer. I gladly acknowledge the courtesy of the Director in continuing to grant the necessary facilities. It will be found that some points differ from a report made on this subject in the winter before the Michigan Academy of Science (Annual Report, 1909) as I have been able to make additional experiments this season.

cence of the sex products the animals lie expanded on the bottom or suspended, and may remain so as long as the light conditions are the same, full darkness having set in. It is probable that much of their prey is captured at this time. As the light grows brighter above, they again move about until they get into weaker light which generally takes them into lower regions or into shaded places, in weak or subdued light. Whenever disturbed, especially by change of light intensity, this medusa swims about in all directions, stopping to float down with expanded tentacles and inverted bell. Again it displays a most striking behavior; it swims almost vertically to the surface of the water by pulsations of the muscular bell, turning over at the surface, expanding and gracefully floating down. Much has been made of this particular behavior by nearly all those who have observed *Gonionemus* for some time. It has been referred to as "fishing" and "surface reaction," the latter term being more satisfactory because less anthropomorphic. The main feature of this behavior is the swimming up toward the surface and floating passively down again after turning over at the surface. This may be renewed as long as the same stimulus acts, or until the condition of the medusa changes so that it no longer responds.

From the foregoing it will be readily understood that these medusæ are sensitive to light influences, getting away from strong light — especially during the earlier part of the day and afternoon — later again moving up toward the fading light. In general, Yerkes,[2] who has made most observations on the reactions of *Gonionemus*, says: "Clearly, the animals are attuned, so to speak, to a certain range of light intensity, and are negative in their reactions to higher intensities." Any marked change in this intensity causes locomotion which under natural conditions brings the medusa into the light suitable for its life processes. Whether this optimum intensity is constant or changes with the activities of the animal has not been determined, but ordinary observation indicates that its range is not very wide; it may be called weak light.

On account of the influence of light on these medusæ they collect in the weaker light of an ordinary glass aquarium placed

[2] *Amer. Jour. Physiol.*, 1903, Vol. IX., page 286.

before a window (cf. Fig. 1). If the light is still stronger than their normal they will continue in their attempt to get farther away. When the aquarium is evenly lighted with subdued light the medusæ are evenly distributed and generally at rest. This may be brought about by darkening the window, and the room if necessary, until the light is uniformly weak. If, now, the side

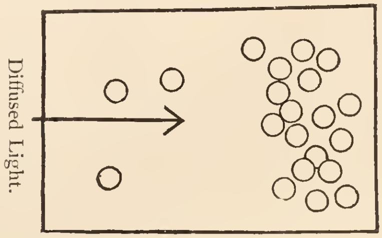

Fig. 1. Top View.

of the aquarium away from the window is darkened still more, then the medusæ are again set into activity, moving about until, after some minutes, they will be found collected in the side of the aquarium near the window.[3] In nature there is probably no collecting in groups, as they are not confined.

Directed Movements.

The main question in my mind has always been whether these medusæ are really directed by light, or properly oriented, even if they could keep the course, *i. e.*, continue oriented or directed. My own experiments have led me to believe that the movements of *Gonionemus* in response to light are not so definitely directed by light as has heretofore been held, and that quantitative differences near their optimum constitute the natural light stimulus. In regard to directed movement, Yerkes[4] says: "It is impossible because of the form of the medusa and its mode of locomotion, that the direction of its movements be as accurately determined by light stimulation as are those of . . . other animals whose structure permits of more accurate orientation in reference to the source of light." While no doubt in a measure true, to me it seems that this statement is not wholly borne out by the fact that it can swim

[3] Because of the observation above I cannot agree with Morse that *Gonionemus* is not positively phototactic.

[4] *Amer. Jour. Physiol.*, 1902, Vol. VI., p. 448.

in nearly straight lines when coming to the surface, in the so-called surface reaction. In fact, the only stimulus to which it seems to respond in pretty straight lines is gravity, though the question of the influence of light in the "surface reaction" is difficult to decide.[5] Yerkes's statement[6] "that the direction of its movement is definitely determined by light" is based on analogy and not on experiment. In this paper[7] such expressions as "movement toward the source of light," and "strong light . . . soon repels the animals"; again, "an animal passes from the shadow into the sunlight" (page 305), I do not take to mean that the animals swam directly toward or from the light. However, if this is meant, the strongest argument in favor of the medusæ's swimming in a direct line not vertical is (page 282) where a medusa inhibited by strong light, starting up again, "usually turns in such a way as to move back into the shaded region." Morse[8] reports a similar experiment differing in that he observed the movement of medusæ in the sunlit half of the dish, saying, "the medusæ begin to swim in all directions." With this my observations agree. Indeed, in Yerkes's answer to this criticism of Morse's, having repeated the experiment, he says: "I found that when the animals swam so far into the sunlit region before turning over that they were entirely in the sunlight when they came to rest on the bottom of the dish, they moved away from the region of shadow about as often as toward it."[9] In this, then, he agrees with Morse's contention that the medusæ do not turn directly toward the shadow and swim into it more often than away from it. In fact he adds (page 462) "with the light perpendicular to the bottom of the vessel I obtained the same results as Mr. Morse. There was no evidence of the directive influence of light."[10] But Yerkes (page 461) also points out that his infer-

[5] This "surface reaction" has been observed in three species of the genus, geographically far enough removed from each other that it seems to indicate an ancestral character.

[6] *Amer. Jour. Physiol.*, 1903, Vol. IX., page 285.

[7] *Amer. Jour. Physiol.*, 1903, Vol. IX., p. 284.

[8] *Jour. of Comp. Neurol. Psychol.*, 1906, Vol. XVI., p. 454.

[9] *Jour. of Comp. Neurol. Psychol.*, 1906, Vol. XVI., p. 461.

[10] Page 462 Yerkes suggests that the contradiction between himself and Morse in regard to oblique light might disappear if Morse's meaning of the term were more fully explained. Turning to Morse's experiment we find (pp. 453–454) that he used

ence from his original experiment was correct for all medusæ falling on the border between sunlight and shade so that "part of the body is in the shadow."

Does Light Orient *Gonionemus*?

Although *Gonionemus* does not move parallel to the direction of stronger light it has been held that its movements are directed by stronger light and that it thus gets from an unfavorable to a favorable light place by direct responses or movements suited to this purpose. Yerkes says:[11] "This is apparently accomplished by the more forceful and earlier contraction of that side of the bell farthest away from the shadow." In the case of other stimuli (tactual and electrical) he had demonstrated this but not in the case of light. Though, page 285, we read: "Observation indicates that the side of the organism which is exposed to the most intense light contracts first and most strongly thus forcing the bell over," yet there is scarcely the weight of proof in this observation. In a later paper Yerkes[12] says: ". . . brilliant illumination of one side of the bell . . . brings about movement toward the region of lower illumination." This is based on an experiment of throwing sunlight on part of a medusa. He gives 66 per cent. as turning toward the region of lower illumination.

Morse[13] restates the same explanation of the turning mechanism, and from the experiment of mutilating one side of the medusa shows that by the resulting one-sided contraction circle swimming is induced. In a later publication[14] he has shown that light has the same effect, *i. e.*, to turn the animal. Half of a medusa in the dark was illuminated by a vertical beam of light. This caused ". . . the medusa to swim vertically upward, and it was only after it had pulsated three or four times that its path veered from the perpendicular. The result of one hundred trials,

only sunlight falling perpendicularly, and in another experiment in which he used oblique light it had no reference to Yerkes's former experiment. More medusæ would fall in oblique light with bodies partly in the shadow than in vertical.

[11] *Amer. Jour. Physiol.*, 1903, Vol. IX., p. 284.

[12] *Jour. of Comp. Neurol. Psychol.*, 1906, Vol. XVI., p. 461.

[13] *Jour. of Comp. Neurol. Psychol.*, 1906, Vol. XVI., p. 451.

[14] *Amer. Nat.*, 1907, Vol. XLI., p. 683.

upon different individuals in the main" gave 70 per cent. in favor of the view "that light has a directly orienting effect." In considering this experiment we should know how many different individuals were used, and should bear in mind that the time limit for response was from five seconds to three minutes, and that the turning began to show only after several pulsations. This would seem to be different from Yerkes's view which is that the medusæ turn directly on stimulation by strong light.

As my experiments were made before the above results were published, and they favor the view of Yerkes that strong light turns the animal immediately they may be added here. The first test was made by using a horizontal band of sunlight as wide as the aquarium, 1 cm. deep, and a little distance — 5 cm. — from the bottom. Darkening the aquarium momentarily was the means of starting the medusæ swimming up toward the band of light. Usually five or more medusæ were used to begin the experiment. Forty-three per cent. were turned back by the band of light, away from the source; 33 per cent. turned toward the source; and 24 per cent. swam straight through the band of sunlight.[15] Now it was thought that an oblique band of sunlight (similar to Fig. 3) would be more decisive, as one side of the up-swimming medusa would be stimulated, not only more strongly, but in advance of the other. In this case 50 per cent. of the medusæ turned away from the direction of the sunlight and 41 per cent. toward it; 9 per cent. did not respond. A relaxed medusa, allowed to float bell downward, showed a more striking result on touching the oblique band of sunlight. It turned, and after swimming upward a few strokes, floated down, only to do the same on striking the band; the next time it floated through and on emerging below turned in the opposite direction, again away from the band of sunlight, but it continued in a circle which again carried it up through the sunlight.

There is enough difference in methods employed in our experiments to leave no doubt that the medusæ do turn at a sudden transition into strong light, especially when they are in very weak

[15] I am compelled to agree with Morse that the collecting of this medusa in strong sunlight is not a normal reaction, but rather due to previous excessive stimulation of some kind.

light. Morse obtained his result with a limited number of resting or moving medusæ. From the conditions of his experiment we may infer that in some cases he did not get a response in less than three minutes. In my own experiments I rejected any reactions that did not take place within a minute after the stimulus was applied. As to the direction of turning into or away from sunlight there is not so great uniformity. Had I taken a few cases like the one of the relaxed medusa above, I would have gotten high percentages. As it is, I have a large enough result (56 per cent.) to conclude with others that *Gonionemus* turns away from strong light. But on carefully observing this turning it is evident that not in many cases do the medusæ turn in such a way that their continued swimming would take them parallel with the light direction. Not infrequently they turn back into the strong light, as has also been observed by others,[15] or are not turned far enough. Is not Morse's ingenious explanation, given below, also a tacit admission that the mere turning by strong light does not cause a medusa to move parallel to the light direction? This turning, therefore, cannot be considered true orientation, and would not lead to swimming directly away from the source of light. But since it has been shown to be a response to strong light, the question remains as to its use to the organism. In nature the medusæ are probably exposed to sunlight only when they are disturbed and swim to the surface, or when the location of one is exposed as the sun's rays come in a different direction. If now the medusæ were to be oriented and swim away from the light it would take them downward, as Morse[16] has already pointed out. It is to be noticed also that both in nature and in aquaria, the bottom prevents this, and in a measure compels swimming toward the region of lesser illumination if the turning by light has been anywhere within half a sphere. It will be seen that this behavior, repeated, even if no further directed movement takes place, will be helpful in temporary escape from strong sunlight.

Ways of Getting into Optimum Light.

If I have succeeded, so far, in making my position understood the question will naturally arise, How do the medusæ get into

[16] *Jour. of Comp. Neurol. Psychol.*, 1906, Vol. XVI., p. 455.

favorable light areas? Although Yerkes does not hold it so, I believe he has indicated one way in his observation:[17] "When an individual in swimming about chances to cross from the sunlit region into the shadow, it very quickly ceases swimming and sinks to the bottom." In another connection but bearing out the same point, Morse[18] has this to say — "being in motion almost incessantly, and swimming in all directions, it is obvious that sooner or later they will enter the dark area. Once having entered this area, the stimulating effect of sunlight being cut off, they remain as in a trap." Even if we do not hold that only light stimulates, or that optimum light acts like a trap the explanation may hold.

More recently Morse[19] has described a way in which *Gonionemus* may get from a location that is unsuitable with respect to light to a more suitable one. A medusa was placed in the end of an aquarium through which the sunlight was reflected horizontally. The medusa swam to the surface in characteristic fashion, each time bending its upward course a little farther from the vertical, and therefore away from the source of light. Thus ultimately it got to the farther side of the aquarium, into weaker light. The promising feature of this explanation is that it is based on the peculiar habit of the animal — swimming to the surface when disturbed. The other case that Morse records of a "strong swimmer" moving directly toward the less illuminated end of the aquarium I should consider an exception, as in repeating the experiment I have observed that some medusæ move almost directly to the lighter end after proceeding, by stages, to the darker end. In my trials I have found that about 25 per cent. get to the farther end of the aquarium by the method indicated, but instead of its being a regular method of progression it seemed to me to be characterized by irregularity. This may be due to the fact that Morse seems to have worked with few individuals, whereas I placed a number in the aquarium at the beginning of the experiment and added to these as the experiment progressed, so as to get results representative of more than individual be-

[17] *Amer. Jour. Physiol.*, 1903, Vol. IX., p. 282.
[18] *Jour. of Comp. Neurol. Psychol.*, 1906, Vol. XVI., p. 454.
[19] *Am. Nat.*, 1907, Vol. XLI., p. 684.

havior.[20] While the majority of the medusæ in the experiment finally reached the less illuminated end of the aquarium they did so by regularly swimming about, resting longer each time they had progressed farther from the light and a shorter time between swimming intervals that again took them toward the light. A few came to rest in the lighter end of the aquarium, as almost always happens in light experiments.

Now if the medusæ do not swim directly toward weaker light and are not turned definitely in such direction, even after trials, at any time, their collecting in weaker light might still be accounted for by the above explanation, if this could be elevated to the dignity of a method. That is, each time a medusa gets into an optimum light it remains longer, and when in an unfavorable light field remains a shorter time, and thus more and more of them will get together in these optimum places.[21]

From the foregoing it will be seen that there are several ways in which *Gonionemus* gets away from the strong light into an intensity best suited to its activities, without the intervention of tropism or "trial." If its only mode of locomotion, or even the chief one, to stimuli were the up-swimming "surface reaction" then it would plainly be "trial," or "motor reaction."

Change of Intensity as a Stimulus.

In Yerkes's earlier statements [22] about the relations of *Gonionemus* to light the words increase and decrease of light intensity are used, but only in his later answer to Morse's criticisms [23] does he make the statement that he has "abundant evidence that change in intensity of light stimulates the medusa." I had experimentally come to the same conclusion.

When the medusæ are at rest darkening the aquarium or shading one with an opaque object, such as the hand, is sufficient

[20] Once I observed a medusa that seemed to follow pretty regularly a movable slit admitting stronger light into a darkened aquarium. Although it was pronounced I could not confirm the reaction in other specimens.

[21] After writing the above I find Mast ("Light Reactions in Lower Organisms, II., Volvox," *Jour. Comp. Neurol. Psychol.*, Vol. XVII., p. 169) has similarly explained the aggregation of *Volvox* in optimum light.

[22] *Amer. Jour. Physiol.*, 1902–3, Vols. VI. and IX.

[23] *Jour. of Comp. Neurol. Psychol.*, 1906, Vol. XVI., p. 460.

to start movement in a few seconds; again, by throwing stronger light with a small mirror on any medusa it can be made to move about. Indeed, the one or the other of these ways was generally used in my experiments to get motor reactions. Next some experiments were made to determine the height to which *Gonionemus* would swim after a single stimulation by change of light intensity. Eight medusæ were placed in a hydrometer jar 72 cm. deep and 9 cm. in diameter. When they had come to rest in the bottom of the jar they were stimulated by darkening the room until the medusæ could just be seen. They swam to the top, at intervals, somewhat irregularly. The shades were now quickly raised and thus the top of the jar illuminated with strong diffused daylight. Three medusæ swam downward so directly as not to touch the sides of the aquarium — not varying 9 cm. from their course. Five floated down part way and then two turned and swam the last third of the way down. In another trial, out of three at the top one swam down 31 cm. without touching the sides of the glass jar. This, it would seem to me, is in the nature of proof that change of light intensity starts and gravity directs the downward course.

Some Mooted Points.

In regard to the question whether the decrease or the absence of light (darkness) is a stimulus for motion or inhibition there is difference of opinion. Yerkes in his first paper[24] on *Gonionemus* says "Romanes's statement that change from light to darkness is inhibitory of action is not very apt." He adds, it "is merely the absence of any motion producing stimulus." In a later paper on this medusa, however, he[25] says "decrease in light intensity temporarily . . . inhibits activity." Morse[26] from practically the same experiment that Yerkes used concludes that "we have no inhibition of movement in passing from light to darkness. In the dark the stimulating effect of light is absent and hence the movements ultimately cease." Yerkes[27] does not agree with this

[24] *Amer. Jour. Physiol.*, 1902, Vol. VI., p. 445.

[25] *Amer. Jour. Physiol*, 1903, Vol. IX., p. 282.

[26] *Jour. of Comp. Neurol. Psychol.*, 1906, Vol. XVI., p. 453.

[27] *Jour. of Comp. Neurol. Psychol.*, 1906, Vol. XVI., p. 460.

criticism but modifies his former statement to say "a considerable decrease causes a more gradual cessation of activity." I have no doubt that he has the correct solution of the question, as shown by the experiments above, when he says — "the change in intensity of light stimulates the medusa." In other words, then, a change in light intensity not only stimulates a resting medusa to move but it may bring a moving individual to rest. This is in accord with well-known facts in the behavior of other animals.

This leads to another point under discussion, *i. e.*, whether or not "the reactions of a swimming organism are different from those of one at rest."[28] Morse[29] believes they are not and supports his contention with an experiment of letting light fall on one half of a medusa resting in the dark; then on the half of a swimming individual. In swimming up both turned from the vertical. It is clear that the discrepancy is based on a misapprehension. To take Morse's own case as an illustration: the light let fall on the resting medusa set it in motion and beyond this, the light produced the same reaction, as it was really in each case falling on a swimming medusa. Therefore Yerkes's statement above is correct.[30]

Surface Reaction.

While there is no doubt that the up-swimming of *Gonionemus* is directed by gravity as stated by Yerkes,[31] nevertheless light seems to be a more important factor than he holds. Indeed I may say it is a necessary concomitant as may be seen from what follows. That it is not directive Yerkes (page 281) has shown by his experiment of using bottom illumination. The medusæ move up to the surface and turn over normally. But casual observation of the upper surface of the water shows that it is sufficiently illuminated from the bottom to allow the medusæ to come to the top. So I substituted lateral illumination through an opening near the bottom of the aquarium. The aquarium

[28] *Jour. of Comp. Neurol. Psychol.*, 1906, Vol. XVI., Morse, p. 452; Yerkes, p. 462.

[29] *Amer. Nat.*, 1907, Vol. XLI., p. 683.

[30] Other points are covered in foot-notes 3, 10, 15, pages 356, 357, 359, also page 365.

[31] *Amer. Jour. Physiol.*, 1903, Vol. IX., p. 281.

was otherwise darkened on all sides and reflection reduced as much as possible by filtering the water. Now the medusæ swam near the bottom, 8 cm. being the greatest height reached. As a control, bottom illumination was then used and immediately one of the animals swam to the surface and one came near it. Three other experiments were made, and the most striking case was that of one medusa swimming through the light band fourteen times in 72 seconds without reaching top or bottom. When the aquarium was so much darkened that I could not see the medusæ, sudden illumination showed that they had attached by their tentacles to the sides or bottom. Thus the presence of light seems necessary for the regular up-swimming activity of *Gonionemus* and gravity then acts as a stimulus to direct it.

In regard to the part light plays in the surface reaction, Yerkes[32] says: ". . . although light seems to be one of the important conditions for this reaction, it may occur in the absence of light." My experiments just cited show that the last part of this statement is not tenable and that the first part is correct. The chief importance of light in bringing *Gonionemus* to the surface, it seems, is in keeping the medusa negative to gravity.

Morse[33] incorrectly, believing that Yerkes held that light causes the inversion at the surface, denies this, and concludes "the cause for reaction is not evident." Later[34] he explains the inversion the same as Yerkes had previously done[35] by assuming that the apex of the bell is thrust unevenly above the surface. Now as the apex of the bell is heavier we no doubt agree that gravity causes the inversion, though not as a stimulus.

As the inversion at the surface is preceded by inhibition of contraction the question arises whether this is due to strong light. Yerkes[36] and Morse[37] have observed that medusæ do not stop and turn (invert) when made to swim up against a heavier substance than air, such as a board, *a glass plate*, a layer of olive oil, but they continue to swim against these layers until ex-

[32] *Jour. of Comp. Neurol. Psychol.*, 1906, Vol. XVI., p. 458.

[33] *Jour. of Comp. Neurol. Psychol.*, 1906, Vol. XVI., p. 451.

[34] *Amer. Nat.*, 1907, Vol. XLI., p. 686.

[35] *Amer. Jour. Physiol.*, 1903, Vol. IX., p. 281.

[36] *Amer. Jour. Physiol.*, 1903, Vol. IX., p. 281.

[37] *Jour. Comp. Neurol. Psychol.*, 1906, Vol. XVI., pp. 450, 451.

hausted. The fact that inhibition and turning do not take place under glass indicates that light does not cause either. The above observations suggested to me that contact of the apex of the bell with air may cause cessation of movement. This idea is apparently supported by holding a layer of air imprisoned under a petrie dish cover some distance below the surface of the water. The animals respond the same as at the surface. Nevertheless, longer observation of the behavior suggests that it is after all, perhaps, nothing more than the recoil of a last ineffective stroke; something as when a person, finding one less step than he expected at the top of a stairway, does not immediately contract his muscles for another step but loses his equilibrium. Light not being the cause of the inversion (with Morse[38]), nor of inhibition, no further discussion is warranted here.

Are the Medusæ Directed by Light Rays?

Morse[39] has decided from an experiment with oblique illumination over the end of a shaded aquarium, because the medusæ collect in the ray-direction-end of the aquarium rather than in the shaded end, that "the direction of the ray of light is the important

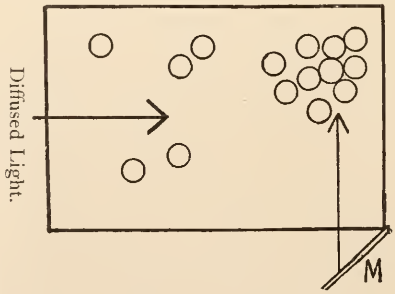

Fig. 2. Top View.

factor in orientation." Has he not left out of consideration another important factor, that of light intensity in the aquarium? Change of intensity has already been shown to be the important stimulus in reactions to light, nevertheless, it seemed worth while to test whether it is ray direction or intensity that determines where the

[38] *Jour. Comp. Neurol. Psychol.*, 1906, Vol. XVI., pp. 450, 451.

[39] *Amer. Nat.*, 1907, Vol. XLI., p. 684.

medusæ will collect. The following experiments were tried: The aquarium used in previous experiments was placed before an open west window at three o'clock in the afternoon, in good diffused daylight. In fifteen minutes the majority of the medusæ had retreated to the end of the aquarium away from the window (Fig. 1, p. 356). Now a large mirror (*M*, Fig. 2) was placed vertically against one corner of the aquarium away from the window, so as to throw light across the end of the aquarium. In fifteen minutes most of the medusæ had collected in the opposite corner of the aquarium away from the window and where the light was least intense. The mirror was now placed at this corner and record again made in fifteen minutes. Many of the medusæ were scattered about, but again there was a larger number collected in the

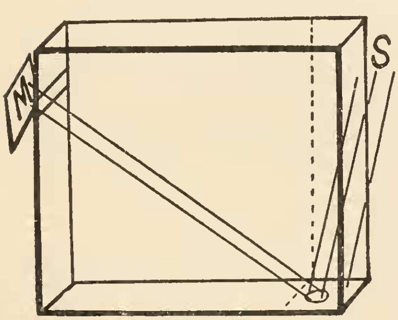

Fig. 3.

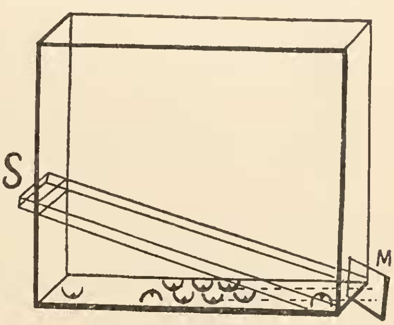

Fig. 4.

corner farthest from the sources of light. In two other experiments a sort of spot-light effect was produced, by having the aquarium darkened except at one end, and a vertical strip (Fig. 3) at one side next the open end so as to throw sunlight across the open end diagonally. There was also a slit near the top of the closed end of the aquarium for a band of sunlight or a mirror beam. The medusæ gathered farthest from the source of light when sunlight was passed through the end of the aquarium. Now crossing this sunlight by a beam from a small mirror, through the slit, made the medusæ leave the place where the light overlapped — where it was more intense. The position of the sunbeam and mirror was reversed with a corresponding result. In this case the mirror was held high enough so that its circumscribed area of reflected light fell on the farther corner of the aquarium, leaving a place of high intensity where the band of sunlight fell, but not so high as that where the two overlapped (Fig. 3). Other portions of the aquarium seemed to be of too low intensity, as the medusæ remained in the lighted portions. The effect of relative intensities was then seen by lowering the mirror so that its beam was projected horizontally across the band of sunlight. Again there were more medusæ in the corner farthest from the two sources of light (compare Fig. 2). In the final test, sunlight was admitted through a slit near the bottom of the aquarium and the mirror placed back of the aquarium in such a position as to throw reflected light obliquely against the sunlight, as it were (Fig. 4). Now the medusæ collected some distance from the back of the aquarium in the region of lesser intensity. Finally, that it is relative intensity and not ray direction is also shown by a former experiment (page 359) where medusæ turned away from an oblique band of sunlight in a darkened aquarium. They turn nearly as often toward as from the source of light. Ray-directing, seems to me, out of the question.

Summary.

1. The medusæ do not usually direct their movements to favorable locations but continue swimming at random until they come into an optimum environment, where they settle down.

2. Intense light turns medusæ away, thus avoiding injury.

3. Change of light intensity is the stimulus for reactions to light. In pronounced decrease, the change of intensity causes inhibition.

4. Relative intensity in the field, not ray direction, determines the place of rest.

5. Light is necessary for the up-swimming activity, though not directive — this being due to gravity.

6. Contact of the bell with air and the accompanying recoil probably causes the inhibition that precedes inversion of the bell at the surface.

Marine Biological Laboratory,
Woods Hole, Mass.,
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